Notes on Salmon River Valley Oreohelicid Land Snails, with Description of *Oreohelix waltoni*

BY

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(5 Plates; 7 Textfigures)

DURING APRIL 1960 I was privileged to collect in the Salmon River Valley of Idaho with the late Munroe L. Walton of Glendale, California, who generously shared his knowledge gained during prior extensive collecting efforts. He personally collected virtually all of the previously described land snails of Western North America. Among our own new finds were two colonies of an undescribed species. Because the colonies were of very limited extent and hence capable of being wiped out by zealous collectors, description of this taxon was deliberately withheld. In August 1974, I participated with Arthur H. Clarke and Robin Vaisey in a survey of potentially endangered land snails of the Salmon River Valley for the Office of Endangered Species (hereafter OES). Recommendations to enable the preservation of several endangered *Oreohelix* species and subspecies, including the taxon described below, have been submitted to the OES. Although it may take some time for the suggested measures to be implemented, description of the new species is now presented, but exact details as to colony location deliberately have been omitted. The data are on file at Field Museum and available for research, but not collecting purposes. The opportunity also is taken to assess the status of taxa grouped as *Oreohelix jugalis* by PILSBRY (1939: 496-499).

Support for this work was received from OES Contracts 14-16-0008-764 and 14-16-0008-843. All drawings were prepared and mounted by Ms. Elizabeth Liebman. The scanning electron microscope (hereafter SEM) photographs in Figures *8* to *36* were taken by the author using a Cambridge S4-10 Stereoscan purchased for Field Museum of Natural History under support of NSF Grant BMS72-02149 A01. I am deeply indebted to Fred Huysmans for his care and skill in maintaining the SEM and preparing the photographic prints, to Dorothy Karall for mounting these into plates, and to Barbara Walden and Jayne Freshour for help with the manuscript preparation. Dr. Marc Imlay and other staff of the OES have contributed greatly to this work.

SPECIES CRITERIA IN *Oreohelix*

Generally a combination of size, proportions, color, and sculpture of the shell has been used to differentiate populations. In a series of studies spanning four decades, PILSBRY (1905, 1916, 1917, 1934, 1939) pointed out several differences in the terminal genitalia and radula. Unfortunately, no detailed revision of the genus incorporating his many suggestions as to taxonomic criteria has appeared. The species of *Oreohelix* show a great range of variation in shell, often illustrate subtle differences in ecology, and are highly colonial in occurrence. Usually only one species is found at a given site. Within a single canyon, species will be ecologically isolated. For example, in Gallatin Canyon, along the West Gallatin River in Montana, *Oreohelix subrudis* (Pfeiffer, 1854) is found under small logs in forest, while on steep treeless slopes under rocks *Oreohelix yavapai mariae* Bartsch, 1916 is common. Similarly, along John Day Creek, north of Lucile, Idaho, *O. strigosa strigosa* (Gould, 1846), *O. haydeni hesperia* Pilsbry, 1939, and *O. waltoni*, spec. nov., occur in quite different situations, respectively, scattered stones and logs in forest near the stream, buried in large limestone talus, and under scattered lava rock piles on open grassy hillsides. The structural and physiologic correlations with these habitat preferences are unknown at present, but any revision of at least the northern *Oreohelix* will have to deal with ecology as a basic parameter.

As background information to the systematic changes reported later in the paper, the opportunity was taken to compare the shells and anatomy of *Oreohelix strigosa strigosa* (Gould, 1846) and *O. vortex* Berry, 1932 collected from the same rock slides at White Bird, Idaho. The total extent of these colonies is less than 150 yards. Shells are shown in Figure 1, and the genitalia are drawn to the same scale in Figure 2. Typical specimens are readily separable on shell characters. *Oreohelix vortex* is smaller, has a more open umbilicus, less impressed sutures, fewer whorls, an angled or weakly keeled periphery, and two well defined spiral color bands; *O. strigosa* is a larger, somewhat higher shell, with more impressed sutures, a narrower umbilicus, usually no peripheral angulation, often more impressed sutures, and generally two narrower spiral color bands. Many shells of the Idaho *O. strigosa,* however, have a generally rufous tint that makes them virtually identical in color to darker specimens of *O. vortex*. Typical examples of this were shown by Pilsbry (1939: 421; fig. 279, 10-11). Table 1 presents data on size and shape variation in samples of the two species from the same slide at White Bird. There is no overlap in terms of shell diameter, but moderate overlap in other features. In Figure 1, a small (top row) and large (middle row) *O. vortex* are compared with one of the smallest *O. s. strigosa* (bottom row). All shells are drawn to the same scale.

In addition to the basic size and shape differences, *Oreohelix vortex* has the columellar lip generally much less reflected than in *O. strigosa* (see right side of Figure 1). There are also differences in shell microsculpture (Figures *11*-*13*. In *O. vortex* (Figure *11*) the microspiral ridges do not extend past the nuclear whorls, while in *O. strigosa* (Figures *12*-*13*) they continue well past the nuclear end, are more clearly interrupted by radial ridging, and apparently are slightly more evenly spaced.

The radulae show an obvious difference. The lateral teeth of *Oreohelix vortex* (Figures *21*-*22*) are strongly bicuspid, while in *O. strigosa* (Figure *18* and see Pilsbry, 1905: plt. XXII, fig. 1) they are unicuspid.

Data on many anatomical differences are summarized in Table 2 and shown in Figure 2. The differences in ovotestis lobe shape, size, and position relative to the coiling plane are obvious. In *Oreohelix vortex* (Figure 2*b*) the lobes (G) are spread out along the tube with few subdivisions in a lobe, and they are angled to the shell axis. In *O. strigosa* (Figure 2*a*), the lobes are organized into a very

Table 1

Variation in *Oreohelix vortex* and *Oreohelix strigosa*

Locality	*Oreohelix vortex* White Bird, Idaho	Types of *Oreohelix vortex*	Types of *O. flammulifer*	*Oreohelix strigosa* White Bird	*Oreohelix strigosa* West bank at Lucile
Date collected	IV-23-1960	1890's	1890's	IV-23-1960	IV-21-1960
Museum #	FMNH 117894			FMNH 117898	FMNH 117888
Number of adults	44	9	10	21	7
Height	7.58 ± 0.12 (6.3-9.1)	7.28 ± 0.14 (6.6-8.0)	7.86 ± 0.12 (7.3-8.3)	11.39 ± 0.26 (9.3-13.4)	11.81 ± 0.49 (9.9-13.8)
Diameter	13.18 ± 0.13 (11.75-14.95)	13.41 ± 0.16 (12.6-14.2)	14.87 ± 0.18 (13.8-15.5)	18.06 ± 0.27 (16.2-20.3)	19.29 ± 0.31 (18.2-20.7)
H/D ratio	0.574 ± 0.0006 (0.481-0.680)	0.544 ± 0.01 (0.478-0.603)	0.529 ± 0.008 (0.500-0.576)	0.630 ± 0.011 (0.549-0.730)	0.611 ± 0.020 (0.547-0.717)
Whorls	5.19 ± 0.03 (4¾-5½)	5.39 ± 0.03 (5¼-5½)	5.36 ± 0.53 (5-5½+)	5.65 ± 0.06 (5-6¼)	5.59 ± 0.05 (5⅜-5¾)
Umbilical width	3.62 ± 0.05 (2.9-4.65)	3.98 ± 0.09 (3.5-4.3)	3.89 ± 0.07 (3.6-4.3)	4.10 ± 0.12 (3.2-4.8)	5.51 ± 0.11 (5.2-6.0)
D/U ratio	3.67 ± 0.06 (2.98-4.72)	3.38 ± 0.06 (3.14-3.68)	3.83 ± 0.07 (3.51-4.08)	4.47 ± 0.13 (3.63-5.56)	3.51 ± 0.09 (3.29-3.97)

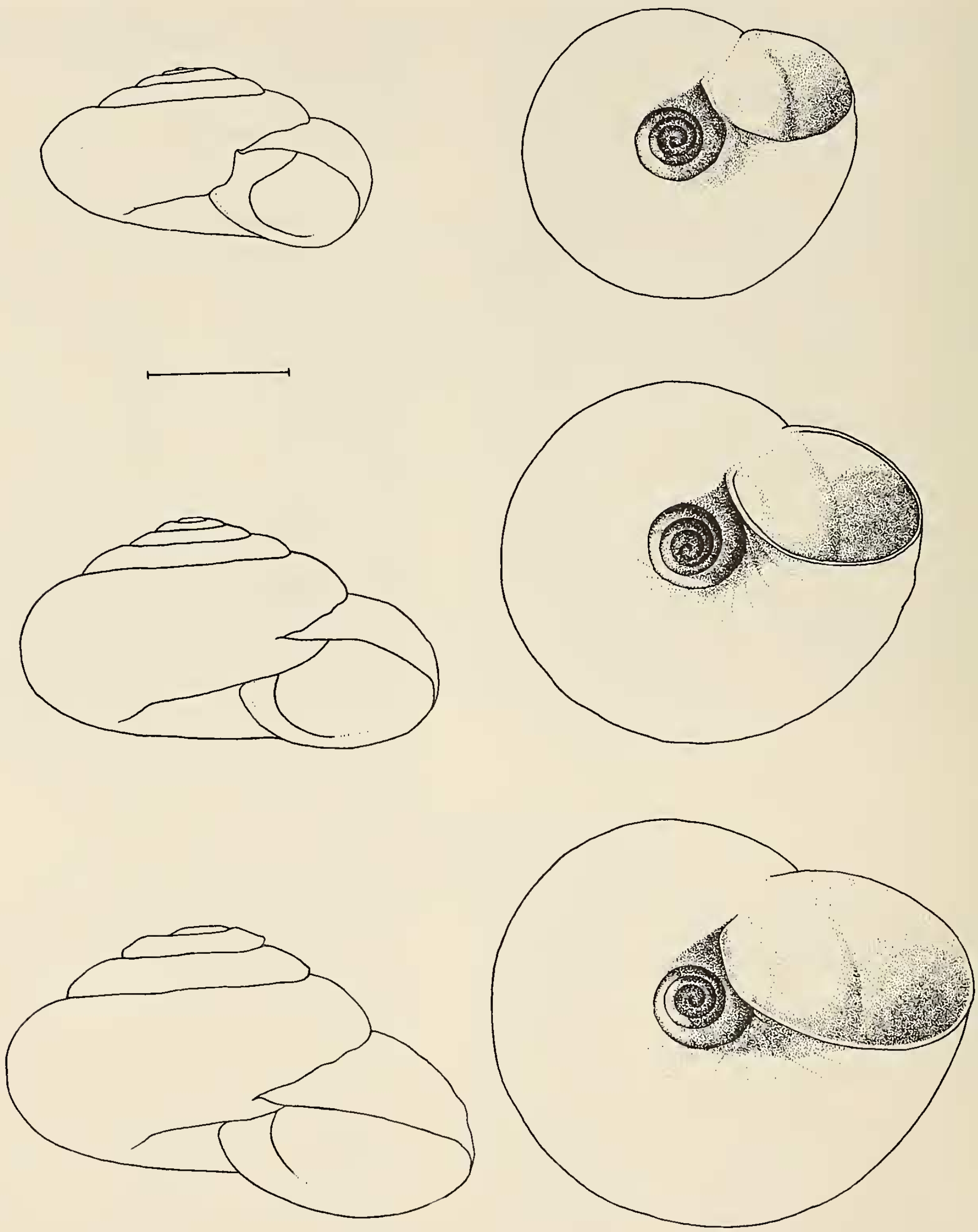


Figure 1

Oreohelix vortex Berry, 1932
and *Oreohelix strigosa strigosa* (Gould, 1846)
Top and middle rows: *O. vortex*. FMNH 117894. Bottom row: *O. s. strigosa*. FMNH 117898. Sympatric at White Bird, Idaho. Collected April 23, 1960. Scale line equals 5 mm.

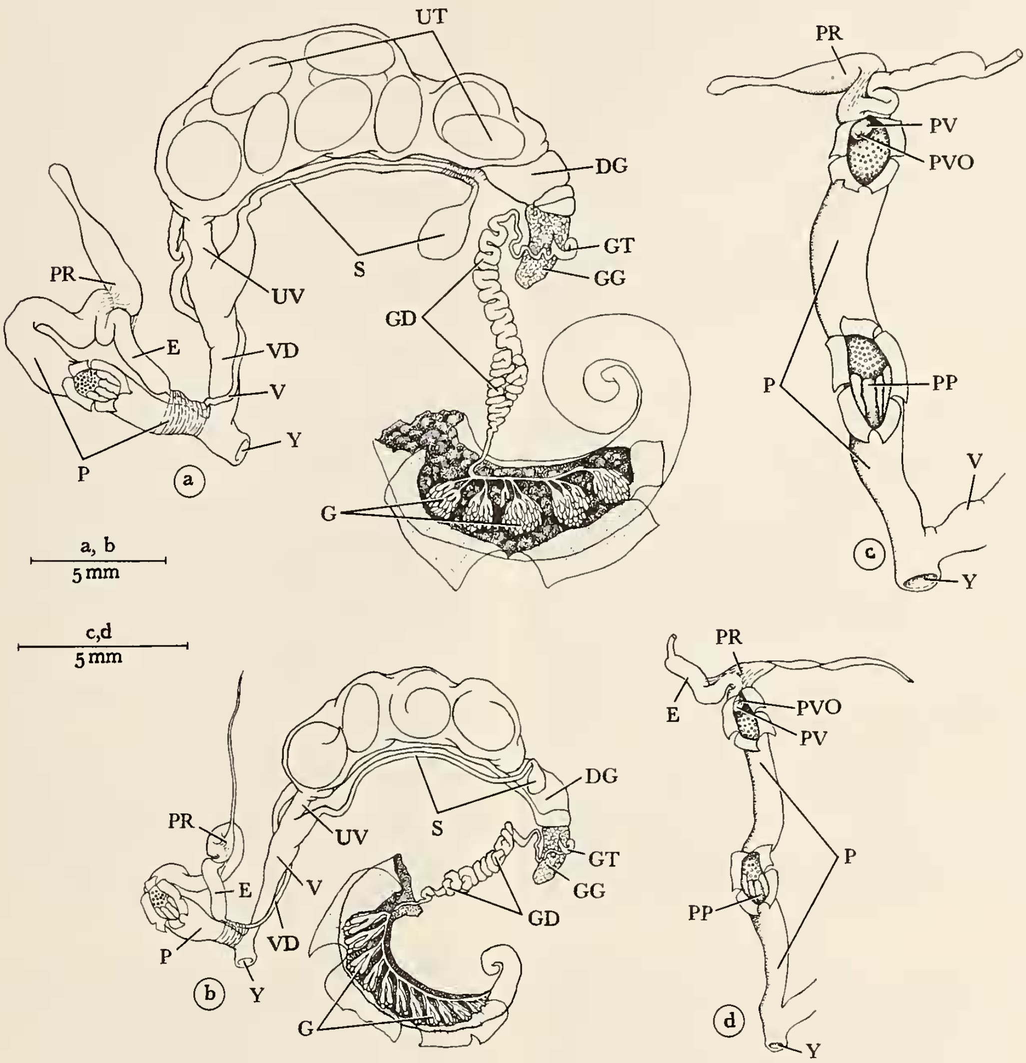


Figure 2

Sympatric *Oreohelix* from the same small rock slide at White Bird, Idaho: *Oreohelix strigosa strigosa* (Gould, 1846). FMNH 170728. Collected August 18, 1974. *a*, genitalia; *c*, penis stretched out and opened. *Oreohelix vortex* Berry, 1932. FMNH 170729. Collected August 18, 1974. *b*, genitalia; *d*, penis stretched out and opened. Scale lines equal 5 mm

Table 2

Differences in sympatric *Oreohelix strigosa* and *Oreohelix vortex*

Character	*Oreohelix vortex* (FMNH 170729)	*Oreohelix strigosa* (FMNH 170728)
Shell size of figured examples		
Height	6.7 mm	12.5 mm
Diameter	11.9 mm	18.1 mm
H/D ratio	0.563	0.691
Whorls	5¼	5⅜
Umbilicus	3.9 mm	3.6 mm
D/U ratio	3.05	5.03
Lateral teeth of radula	bicuspid	unicuspid
Ovotestis lobes	clumped and slanted to shell axis	separated and perpendicular to shell axis
Embryos in uterus	4	11
Diameter of embryos	2.75-3.14 mm	3.53-3.79 mm
Length of GD coiled section	4.1 mm	7.8 mm
Atrium to PR insertion length	2.7 mm	4.6 mm
Atrium to base of uterus	5.6 mm	7.1 mm
Penis length:		
Total	8.9 mm	11.8 mm
Ridged	3.7 mm	4.5 mm
Pustulose	5.2 mm	7.3 mm

few clumps that are distinctly spaced out and lie parallel to the shell axis. The lengths of the hermaphroditic duct coiled portion (GD) is only about half as long in *O. vortex,* whereas the distance from the peni-oviducal angle to base of uterine chamber is almost $\frac{4}{5}$ as long in *O. vortex.* In all *Oreohelix* I have dissected, the vas deferens (VD) is bound by connective tissue to the penis. Frequently the epiphallus (E) is slightly kinked and bound to the penial retractor muscle (PR). This thus provides a marker against which the lower margin of the penial retractor muscle can be measured. Although the epiphallus (E) is shown slightly flexed in Figure 2 *a,* measurement of the distance from the peni-oviducal angle to the lower margin of the penial retractor muscle is quite feasible and presents a comparable feature. The length in *O.vortex* is about $\frac{3}{5}$ of the length in *O. strigosa.* Actual penis length shows yet a different proportion, with the stretched out penes (Figures 2 *c, d*), totalling 8.9 mm in *O. vortex,* which is $\frac{3}{4}$ of the length in *O. strigosa.* The proportion of ridged to pustulose areas in the two is essentially identical, about $\frac{2}{5}$ ridged. *O. strigosa* (Figure 2 *c*) has a slightly larger vergic papilla (PV) with the opening (PVO) medial, while in *O. vortex* (Figure 2 *d*) the opening is lateral.

The most obvious difference is in the number and size of embryos contained in the uterine chamber (Table 2), with the much larger, more numerous young in *Oreohelix strigosa.* The specimens figured and measured here were taken in a single small rock slide, isolated by grassy slopes for several yards in each direction from other slides containing the species. Other dissected examples did not differ significantly, but no statistical analysis is attempted. Hence there was no question but that sympatric interactions occurred. Specimens taken from the same slide in April 1960 also agreed in basic proportions, although without developed embryos for counting.

The differences in penial structure and proportions are much smaller than between other features in the genitalia, yet material collected by Walton in the 1940's and 1950's, by Walton and Solem in 1960, and by Solem, Clarke and Vaisey in 1974 showed no evidence of hybridization. *Oreohelix strigosa* and *O. vortex* are distinct species. Hence it is concluded that where allopatric populations show significantly greater penial differences than demonstrated above, and these differences are coupled with equivalent shell differences, full species rank is indicated.

Explanation of Figures *8* to *13*

Oreohelix waltoni Solem, spec nov.

John Day Creek, north of Lucile, Idaho County, Idaho. Collected April 22, 1960 by A. Solem and M. L. Walton. FMNH 98141. Paratype.

Figure *8*: Shell apex from dissected paratype × 32

Figure *9*: Shell apex from another paratype × 53

Figure *10*: Early postnuclear sculpture from another paratype × 97

Oreohelix vortex Berry, 1932

Rock slide at White Bird, Idaho County, Idaho. Collected August 18, 1974 by A. Solem and A. Clarke. FMNH 170729.

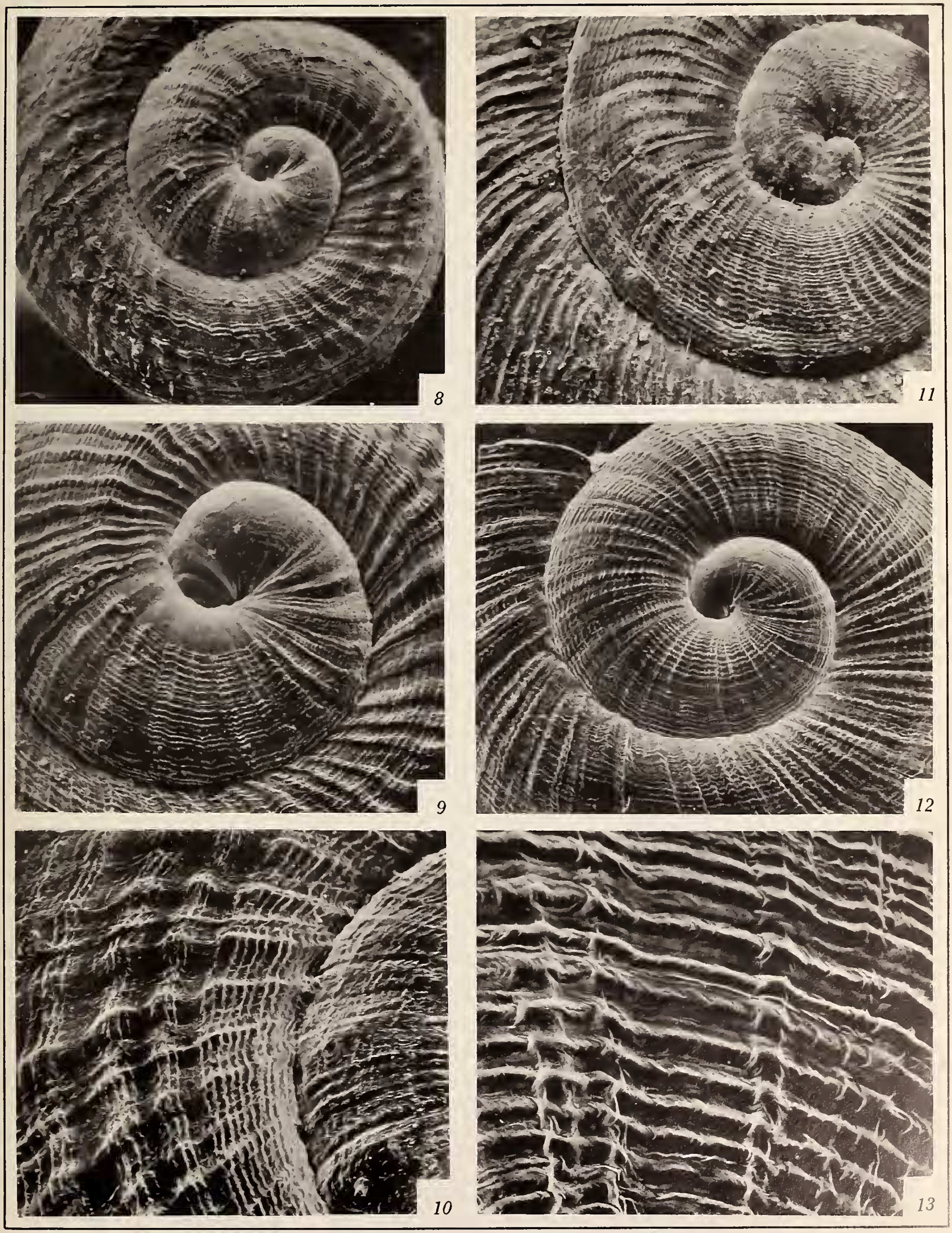
Figure *11*: Shell apex and early postnuclear whorls × 33

Oreohelix strigosa strigosa (Gould, 1846)

Rock slide at White Bird, Idaho County, Idaho. Collected August 18, 1974 by A. Solem and A. Clarke. FMNH 170728.

Figure *12*: Embryonic shell sculpture × 34

Figure *13*: Detail of embryo shell sculpture × 197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GASTROPODA

Sigmurethra

Oreohelicidae

Oreohelix Pilsbry, 1904

Oreohelix waltoni Solem, spec. nov.

(Figures 3, 4b, 5c, 6d, *8 - 10*, *14 - 17*, *30*)

Diagnosis: Shell small, widely umbilicated, averaging less than 5 whorls, postnuclear sculpture of prominent, somewhat irregular and erratically spaced protractive radial ribs. Penis relatively short, pustulose region moderately longer than ridged, epiphallus long and tapering, entering laterally into penis through a short vergic papilla. Central tooth of radula tricuspid, laterals 6 or 7 in number, bicuspid with prominent ectocone, marginals 14 or 15, bicuspid with ectoconal splitting on outer marginals.

Oreohelix waltoni is a very distinctive species in both shell and genital characters. *Oreohelix peripherica* (Ancey, 1881) and *O. idahoensis* (Newcomb, 1866) have usually stronger radial ribbing on the shell, higher spires and much narrower umbilici, less prominent (*O. idahoensis*, Figure *26*) or no ectocones (*O. peripherica*, see Pilsbry, 1916: 350) on the lateral radular teeth, and the genitalia have a shorter epiphallus, different penial vergic papilla, and quite different orientation of the ovotestis lobes (Figure 7*a*). *Oreohelix vortex* has a similar shell shape and umbilical size, but has a larger shell that lacks the major radial ribbing, has a much longer penis with longer pustulose region, proportionately shorter epiphallus, and distinctly longer vaginal region.

Description: Shell (Figure 3) small, diameter of adults 8.3-10.9 mm (mean 9.42 mm), with 4⅜ to 5¼ (mean 4.76) normally coiled whorls. Spire evenly but variably protruding, last whorl descending more rapidly, height of shell 4.55-7.0 mm (mean 5.77 mm), H/D ratio 0.511-0.711 (mean 0.613). Apical whorls about 2 to 2⅛, sculpture basically of irregularly spaced microspiral cords that continue across low radial swellings. Often microspirals absent from apex tip and inner suture. Postnuclear whorls with microspirals continuing in unworn areas, radial swellings becoming larger and more sharply defined, but never becoming completely regular and varying greatly in height from suture to umbilicus. Body whorl with angled to weakly keeled periphery, descending moderately just before aperture. Columellar lip reflected slightly and noticeably thickened at adulthood, parietal callus often thick

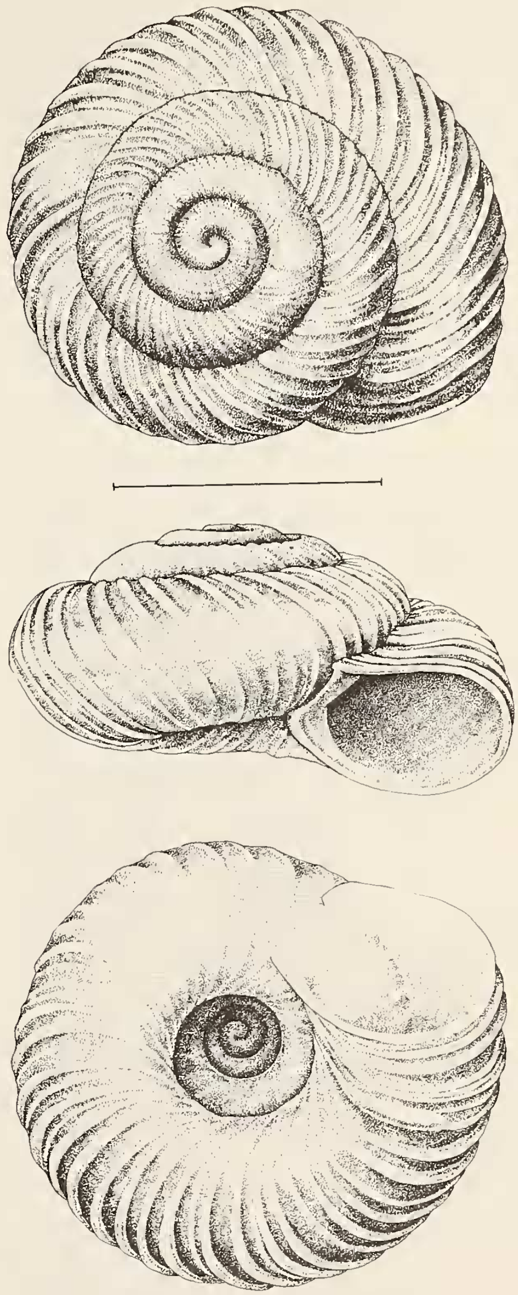


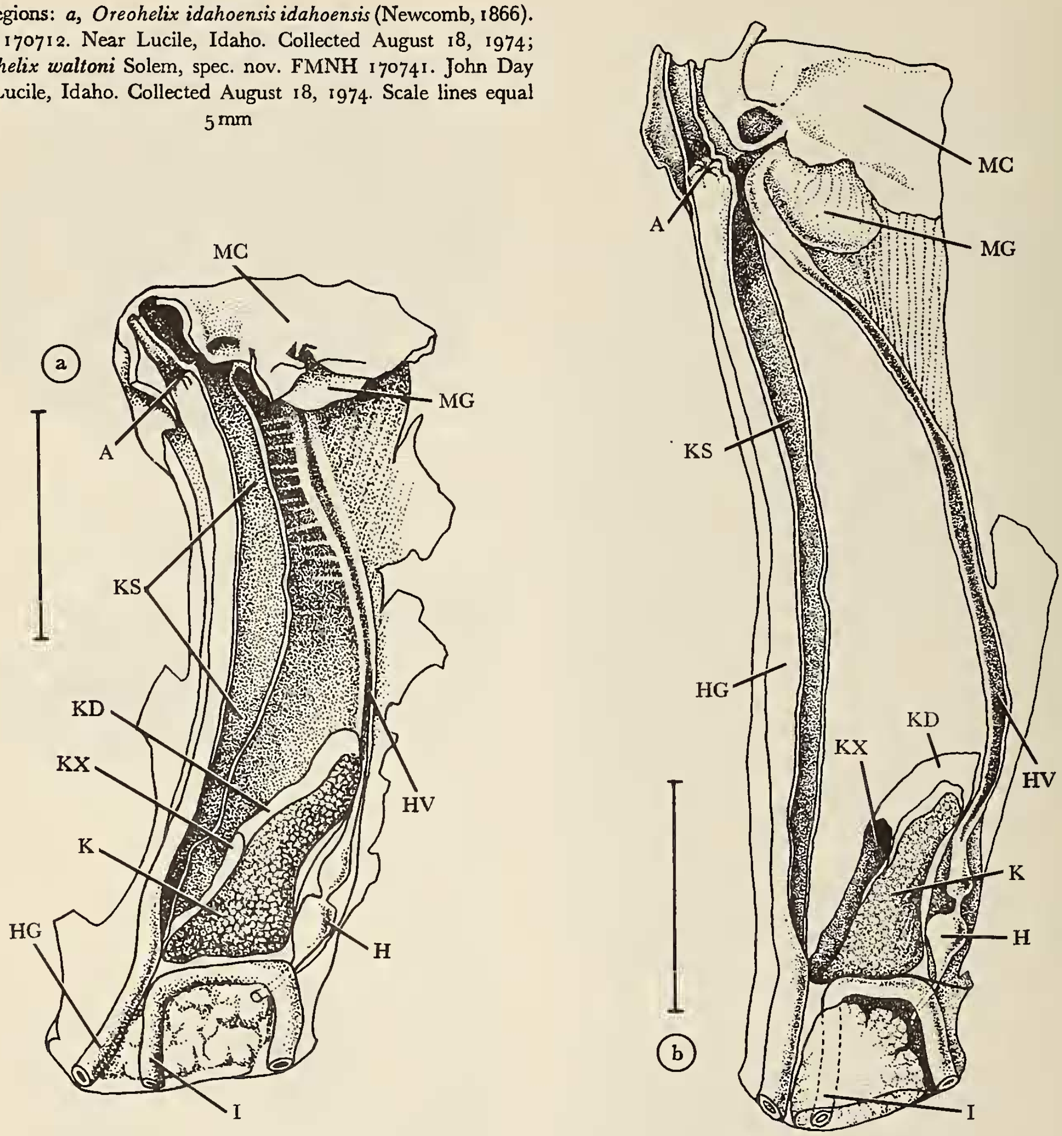
Figure 3

Oreohelix waltoni Solem, spec. nov.

Holotype. FMNH 182000: *a*, top view of shell; *b*, side view of shell; *c*, bottom view of shell. Scale line equals 5 mm

Figure 4

Pallial regions: *a*, *Oreohelix idahoensis idahoensis* (Newcomb, 1866). FMNH 170712. Near Lucile, Idaho. Collected August 18, 1974; *b*, *Oreohelix waltoni* Solem, spec. nov. FMNH 170741. John Day Creek, Lucile, Idaho. Collected August 18, 1974. Scale lines equal 5 mm



Explanation of Figures *14* to *19*

Oreohelix waltoni Solem, spec. nov.

John Day Creek, north of Lucile, Idaho County, Idaho. Collected August 18, 1974 by A. Solem and A. Clarke. FMNH 170741

Figure *14*: Part row of radular teeth, central tooth 2nd from upper left corner × 285

Figure *15*: Central and first lateral teeth × 1045

Figure *16*: Transition between lateral and marginal teeth × 645

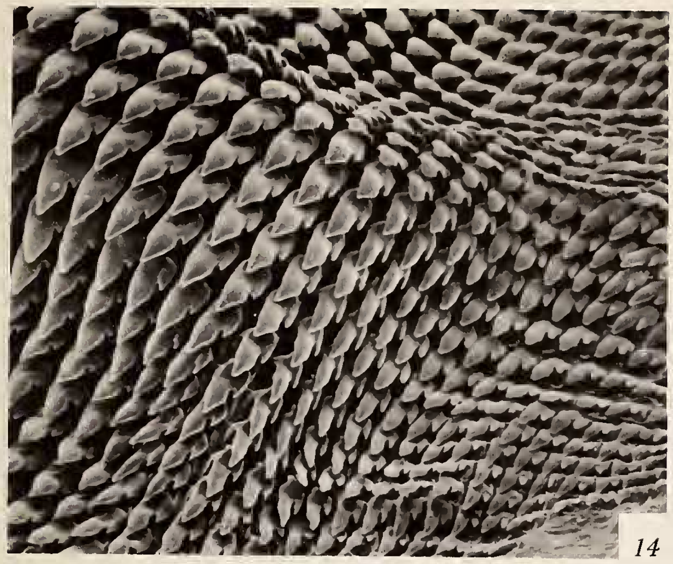
Figure *17*: Outer marginal teeth × 850

Oreohelix strigosa strigosa (Gould, 1846)

Rock slide at White Bird, Idaho County, Idaho. Collected August 18, 1974 by A. Solem and A. Clarke. FMNH 170728

Figure *18*: Central and early lateral teeth × 480

Figure *19*: Marginal teeth × 955



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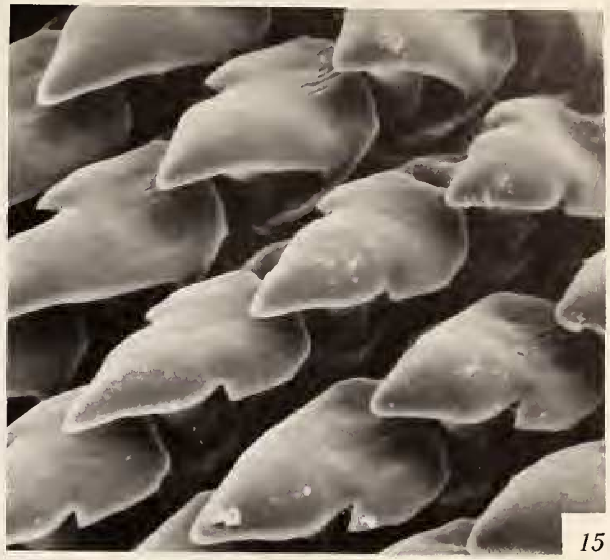

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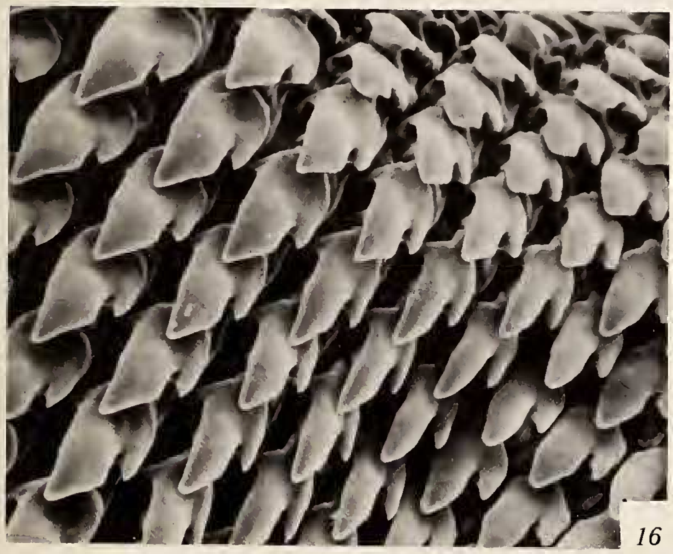

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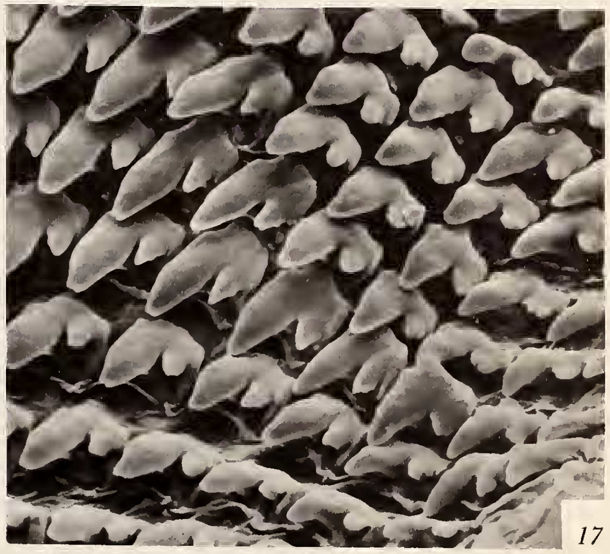

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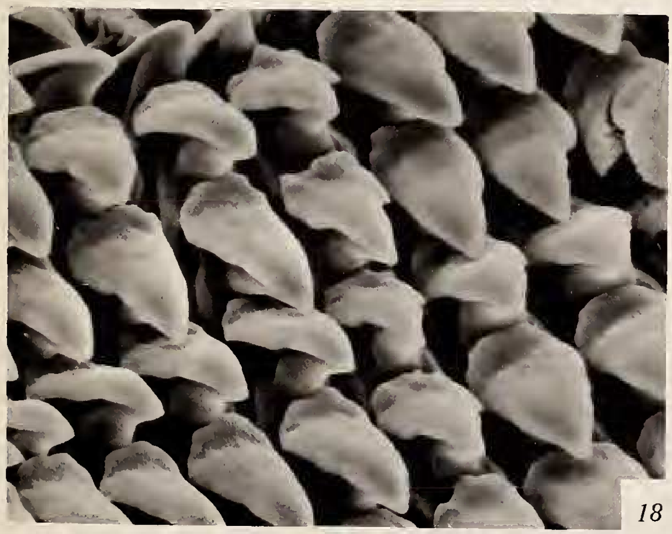

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with rolled edge. Aperture ovate, flattened above, inclined about 30° from shell axis. Umbilicus 2.0-3.7 mm wide (mean 2.91 mm), decoiling regularly, contained 2.65 to 4.43 times (mean 3.26) in the shell diameter. Height of holotype 5.45 mm, diameter 9.4 mm, whorls 4⅝, D/U ratio 3.13.

Pallial region (Figure 4 *b*) with well developed mantle gland (MG) that is heavily vascularized from pulmonary vein (HV). Kidney (K) and heart (H) typical, intestinal loop (I) indenting inner kidney margin. Hindgut (HG) without unusual features, anus (A) opening into a clear gutter through pneumostome. Kidney (K) elongately triangular, almost reaching hindgut. Closed portion of ureter (KD) very short, extending less than half length of kidney, opening (KX) into a long reflexed ureteric sulcus (KS), bordered by a low renal ridge.

Genitalia (Figures 5 *a*, 5*c*, 6*d*) with comparatively few ovotestis lobes (G) that are angled to the shell axis. Hermaphroditic duct (GD) relatively loosely coiled, talon (GT) and albumen gland (GG) typical. Latter enlarged greatly in April (Figure 5 *a*) compared with August (Figure 5 *c*) examples. Prostate (DG) typical, uterus (UT) empty in April (Figure 5 *a*), all August examples with four fully formed embryos (Figure 5 *c*), each partly enclosed in a

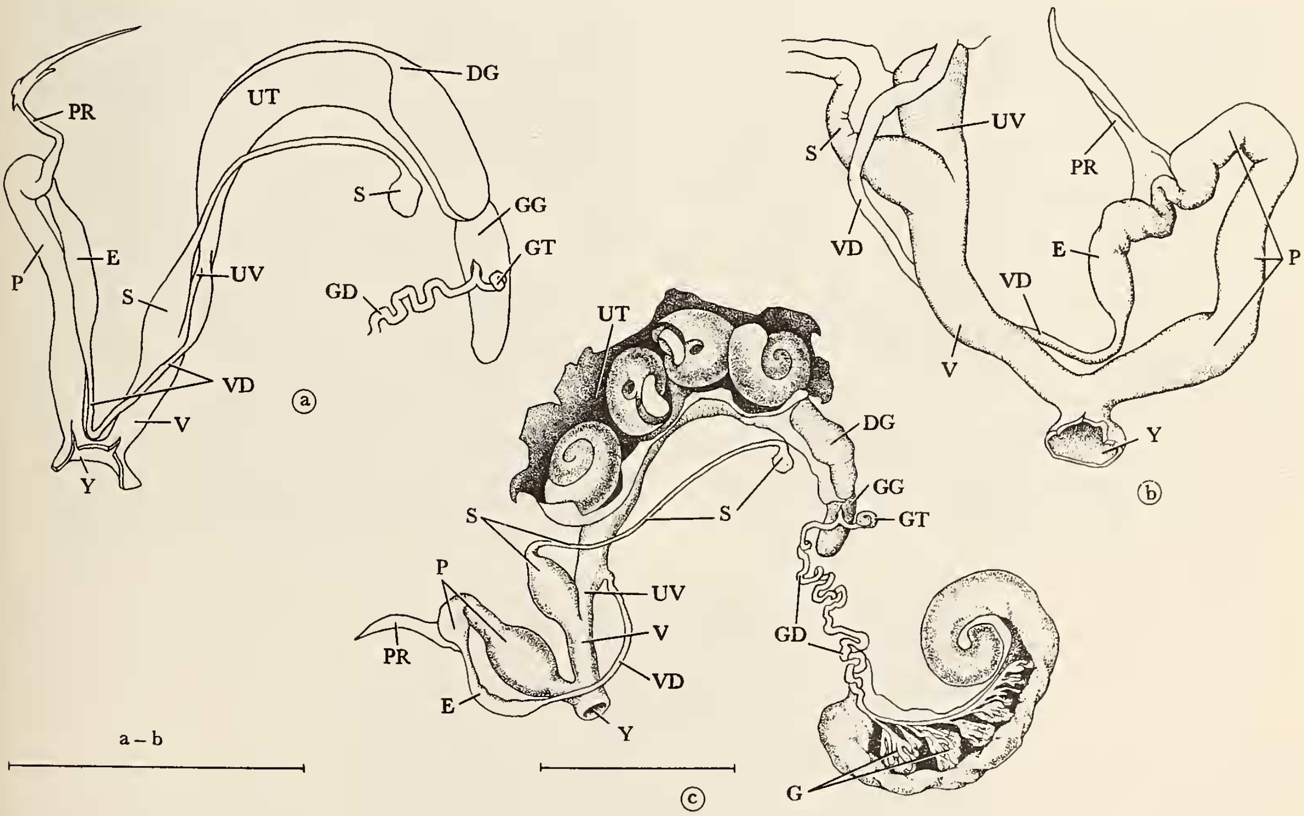


Figure 5

Genitalia: *a*, *Oreohelix waltoni* Solem, spec. nov. Paratype. FMNH 98141. Up John Day Creek, north of Lucile, Idaho. Collected April 22, 1960; *b*, *Oreohelix vortex* Berry, 1932. FMNH 170729. White Bird, Idaho. Collected August 18, 1974; *c*, *Oreohelix waltoni* Solem, spec. nov. Paratype. FMNH 170741. Up John Day Creek, north of Lucile, Idaho. Collected August 18, 1974. Scale lines equal 5 mm membranous sac. Free oviduct (UV) very short, spermatheca (S) with moderately (April) to strongly (August) swollen base, stalk very slender, head expanded, subcircular, lightly bound to area just above uterus apex by connective tissue. Vagina (V) relatively long, without special internal ridging. Vas deferens (VD) normally bound to peni-oviducal angle, expanding gradually into quite slender and long epiphallus. Epiphallus (E) internally (Figure 6 *d*) with single large ridge (EPP) and a series of small pilasters angling apically from this. Penial retractor muscle (PR) inserting partly on epiphallus and partly on penis, with head of penis reflexed so that the penial verge (Figure 6 *d*, PV) points apicad and the pore (PVO) also points apically under normal contracted situation. Penis (P) slender in April (Figure 5 *a*), greatly swollen in August (Fig. 5 *c*) due to enlargement of the basal longitudinal pilasters (PP in Figure 6 *d*). Pustulose zone of penis distinctly longer than ridged area.

Radula with 22 teeth per half row (Figure *14*). Central tooth (Figure *15*) smaller than first laterals, tricuspid, with curved anterior margin, mesocone quite elongated. Lateral teeth about 7, bicuspid with prominent ectocone (Figure *15*), transition to marginals (Figure *16*) occurring at 6th or 7th tooth, involving initial narrowing of mesocone with increased angle to inner edge of cusp, marked separation of ectocone from mesocone and increase in prominence for latter. By the 10th tooth the typical marginal form is reached (Figure *17*, followed by the change to outer marginals involving broadening and shortening of the entire tooth and some sign of ectoconal splitting on the outermost teeth. The pattern of interrow support in the lateral teeth (Figure *30*) involves relatively slight anterior flare and curve on the mesocone.

Holotype: Idaho, Idaho Co., more than 1.6 km up John Day Creek from the Salmon River, north of Lucile. In small lava rock piles on a grassy slope. Collected April 22, 1960 by Alan Solem and the late Munroe L. Walton. Field Museum of Natural History, number 182000.

Paratypes: Additional specimens from the type locality are FMNH 98141, also collected April 22, 1960; FMNH 170741 and National Museums of Canada number 72060 collected August 18, 1974 by Alan Solem, Arthur H. Clarke, and Robin Vaisey. A second colony is located on a steep east facing grassy slope on the west bank of the Salmon River near Lucile, Idaho County, Idaho. Specimens were collected April 21, 1960 by Alan Solem and the late Munroe L. Walton (FMNH 98151) and by Alan Solem on August 19, 1974 (FMNH 170711). Many other specimens from these localities are in the Munroe L. Walton shell collection, now in the Delaware Museum of Natural History, but were not used in preparing the description or analysis of variation.

Remarks: This species is dedicated to the late Munroe L. Walton, naturalist, superb field collector, student of Western North American land snails, and good friend.

Variation in adult examples is summarized in Table 3. The two colonies have quite different exposures and the size and shape differences in the material are statistically significant, in both geographic and allochronic comparisons. Comparing just the 1960 collections, with 94 degrees of freedom, "*t*" is 4.5359 for diameter, 3.5095 for D/U ratio, and 2.4007 for umbilical width, highly significant levels of difference. As typical of semiarid areas, the rainfall in the Salmon River drainage shows great annual fluctuations, so that size differences from year to year would be expected. *Oreohelix* colonies are notoriously variable in size and shape, so no biological significance is attached to these variations.

Structural comparisons with *Oreohelix idahoensis* (Newcomb, 1866) reveal numerous differences. The pallial region in the latter (Figure 4 *a*) is shorter, the kidney is longer, there is more obvious branching from the pulmonary vein, the mantle gland (MG) extension from the mantle collar (MC) is less developed, and the ureteric sulcus (KS) is broader along the hindgut. A surprising feature in the pallial complex of all examined species is the very short

Explanation of Figures *20* to *24*

Oreohelix vortex Berry, 1932

Rock slide at White Bird, Idaho County, Idaho. Collected August 18, 1974 by A. Solem and A. Clarke. FMNH 170729

Figure *20*: Part row of radular teeth × 205
Figure *21*: Central and early lateral teeth × 1025
Figure *22*: Transition from lateral to marginal teeth × 685
Figure *23*: Low angle view of mid-lateral teeth × 1870
Figure *24*: Outer marginal teeth × 935

Explanation of Figures *25* to *30*

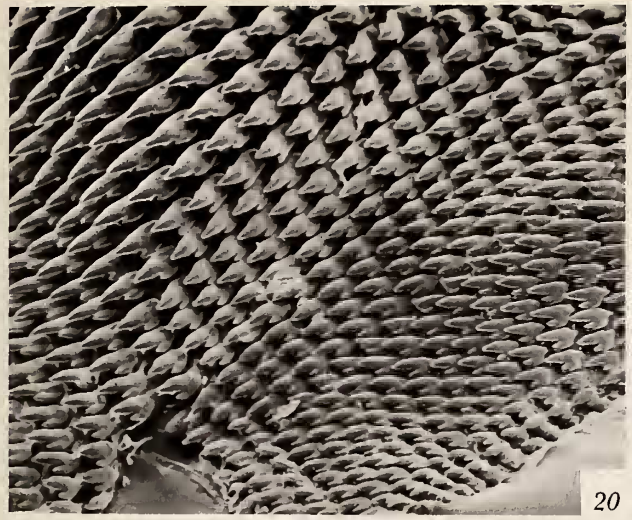
Oreohelix idahoensis idahoensis (Newcomb, 1866)

Lucile, Idaho County, Idaho. Collected August 18, 1974 by A. Solem and A. Clarke. FMNH 170712

Figure *25*: Part row of radular teeth × 250
Figure *26*: Central and early lateral teeth × 870
Figure *27*: Basal plate support system in lateral teeth × 1495
Figure *28*: Outer marginal teeth × 1105
Figure *29*: Basal plates in newly formed lateral teeth × 1075

Oreohelix waltoni Solem, spec. nov.

Figure *30*: Basal plate support system in outer lateral teeth × 1330



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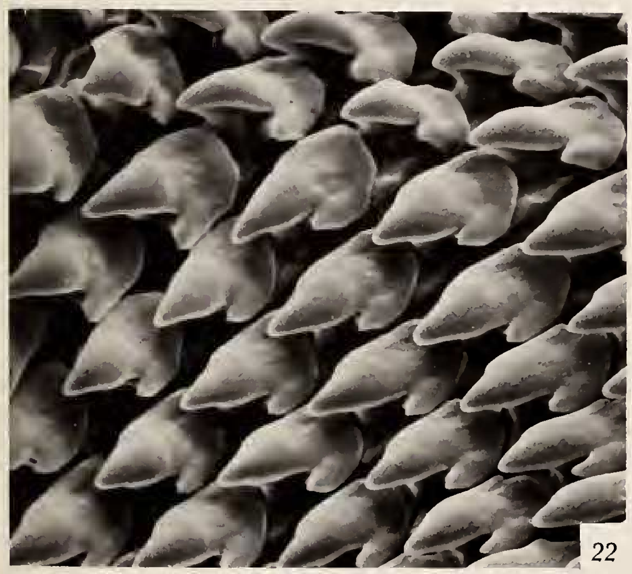

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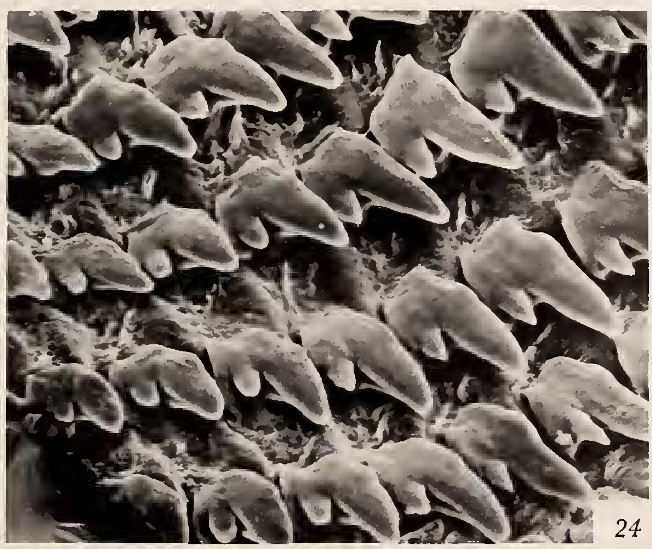

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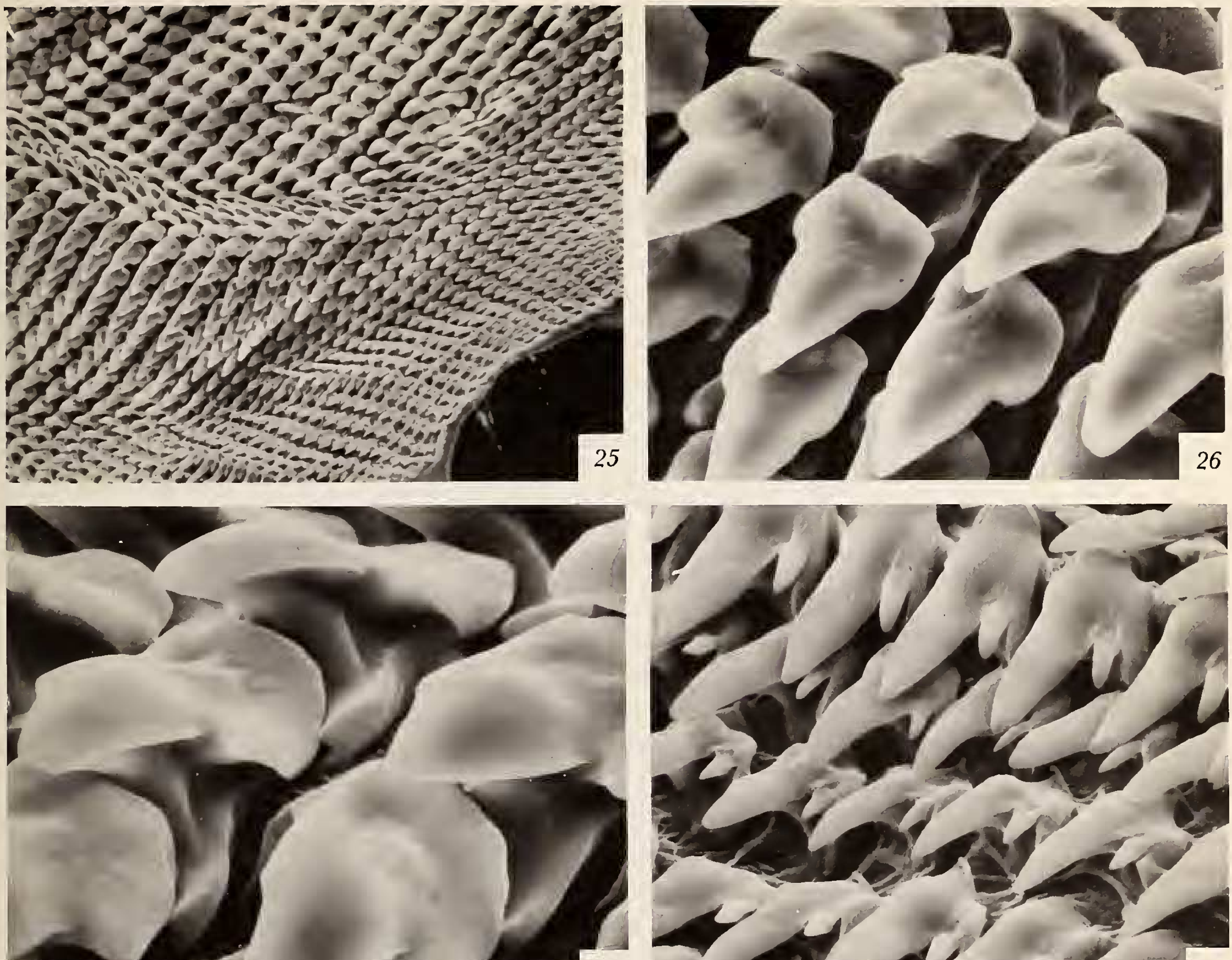
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Table 3

Variation in shells of *Oreohelix waltoni* Solem, spec. nov.

Locality	John Day Creek, north of Lucile		Salmon River at Lucile
Date collected	IV-22-1960	VIII-18-1974	IV-21-1960
Museum #	(FMNH 98141)	(NMC 72060)	(FMNH 98151)
Number of adults	42	5	54
Height	5.78 ± 0.07 (4.9-6.9)	6.24 ± 0.20 (5.8-7.0)	5.72 ± 0.07 (4.55-6.9)
Diameter	9.56 ± 0.05 (8.9-10.45)	10.5 ± 0.25 (9.55-10.9)	9.21 ± 0.06 (8.3-10.5)
H/D ratio	0.604 ± 0.006 (0.533-0.695)	0.595 ± 0.022 (0.532-0.648)	0.621 ± 0.006 (0.511-0.711)
Whorls	4.80 ± 0.027 (4⅜-5¼)	4.98 ± 0.06 (4¾-5⅛)	4.71 ± 0.03 (4⅜-5¼)
Umbilical width	3.03 ± 0.034 (2.6-3.6)	3.39 ± 0.14 (3.0-3.7)	2.78 ± 0.03 (2.0-3.3)
D/U ratio	3.17 ± 0.03 (2.65-3.52)	3.11 ± 0.10 (2.88-3.43)	3.34 ± 0.04 (2.89-4.43)

closed ureter followed by the open groove. This is characteristic of the Ammonitellidae (see Pilsbry, 1939: 561-567). Pilsbry (*op. cit.*: 412) had reported a closed secondary ureter in *Oreohelix*, but Wurtz (1955: 108; fig. 16 in plt. 3) subsequently had illustrated the correct pattern.

In the genitalia (Figures 7 *a* and 6 *c*) there are obvious differences between *Oreohelix* ***waltoni*** and *O. idahoensis* in ovotestis lobation, epiphallus length, penial retractor muscle insertion, vergic papilla shape and pore position (lateral in *O. idahoensis*, Figure 6 *c* and terminal in *O.* ***waltoni***, Figure 6 *d*), and relative lengths of the pustulose and ridged sections. The central radular tooth of *O. idahoensis* (Figure *26*) and the lateral teeth (Figures *26, 27*) have less prominent ectocones, the marginal teeth (Figure *28*) have much longer and narrower mesocones, while the interrow support system (Figures *27, 29*) involves a much larger anterior flare and correspondingly higher basal ridge. The mounted radula has 27 teeth in a half row (Figure *25*), with 20-21 of these marginals.

Oreohelix vortex is much more similar in radular structure (Figures *20-24*), but shows numerous shell and genital differences, which have been discussed in the diagnosis above.

Observations made by Henderson & Daniels (1916: 317) during Northern Utah and Southern Idaho field work in August and September of 1915 help explain the variation in structure between the specimens taken in April and August. They reported that "In the lots obtained after the first few days of September very few embryos were found . . . The summer was hot and extremely dry . . . over ninety days without measurable rain. After the rains commenced on September 2 they became active . . . and large numbers were found in copulation." Thus the fully developed embryos found in all dissected species taken in mid-August and the enlarged nature of the terminal genitalia when compared with the April examples (Figures 5 *a, c*) suggest that at the start of Fall rains the young are shed and mating is initiated. The small albumen gland in August compared with April would suggest that sperm are stored over winter. The April specimens were taken about two weeks after disappearance of snow cover and the snails were moving about. The absence of formed young in the uterus during April suggests that food is accumulated and stored until the end of Spring rains, with egg fertilization and development occurring during the summer droughts, while the snails are in aestivation. The above hypothesized sequence is logical, but requires testing through multiple sampling from populations through the year. To my knowledge, no species of *Oreohelix* has had its life history recorded, leaving major and intriguing problems for investigations by biologists living within its geographic range.

SPECIES of the *Oreohelix jugalis* COMPLEX

Pilsbry (1939: 496-499) grouped *Oreohelix jugalis* (Hemphill, 1890), *O. vortex* Berry, 1932, *O. flammulifer* Berry, 1932 and *O. intersum* (Hemphill, 1890) as three subspecies under the oldest name, *O. jugalis*. *Oreohelix junii* Pilsbry, 1934 also was cited (Pilsbry, 1939: 495) as a possibly closely related species. Subsequently, Hanna &

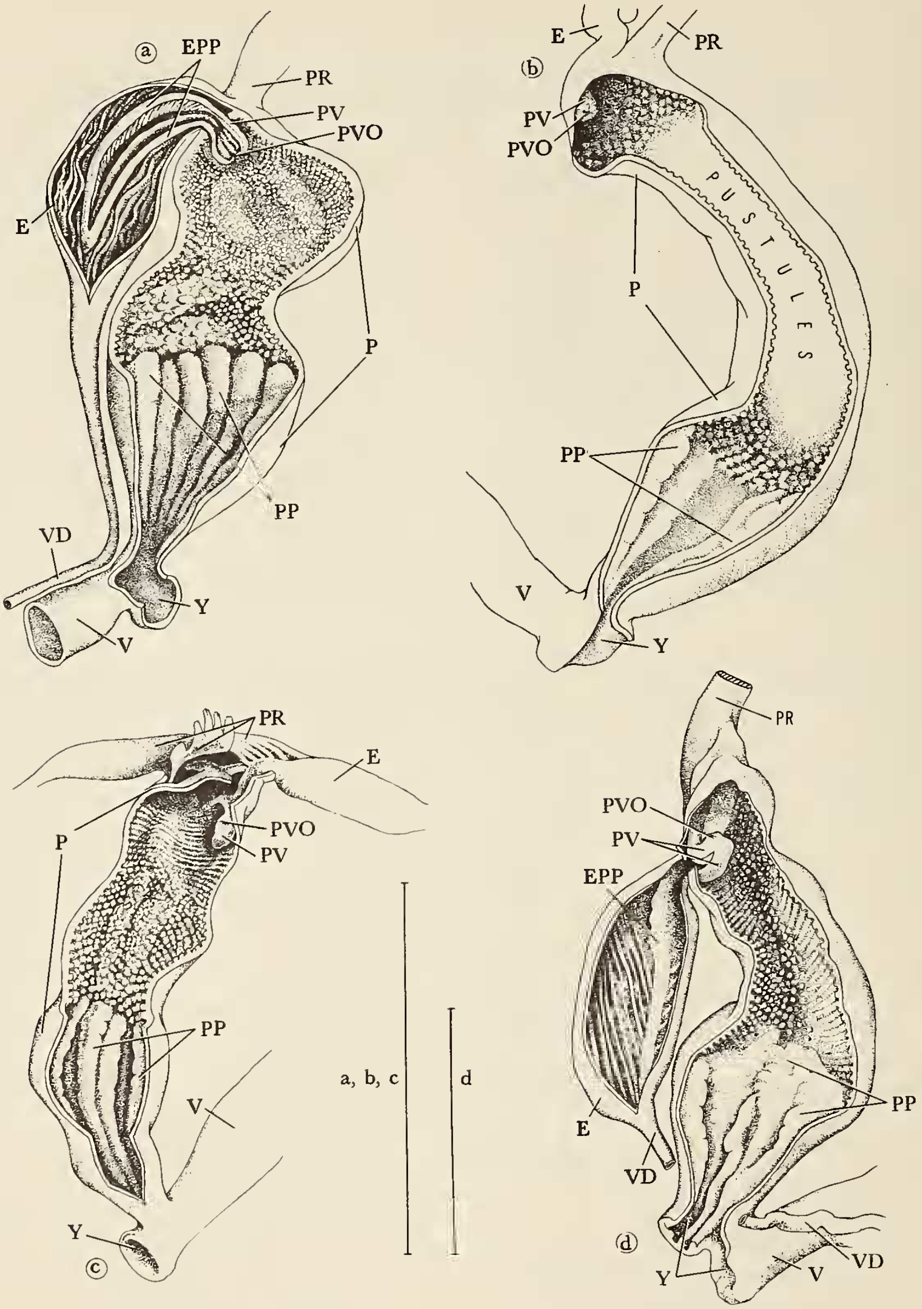


Figure 6

Penial chambers: *a, Oreohelix jugalis* (Hemphill, 1890). FMNH 170742; *b, Oreohelix vortex* Berry, 1932. FMNH 170729; *c, Oreohelix idahoensis idahoensis* (Newcomb, 1866). FMNH 170712; *d, Oreohelix waltoni* Solem, spec. nov. FMNH 170741. Scale lines equal 5 mm

Smith (1939: 385-386, 388-389) placed *O. jugalis* as a synonym of *O. strigosa* and considered that *O. intersum* was a distinct species. Smith (1943: 538) later reversed himself. He considered that *O. jugalis* was a distinct species and reported the first definite locality for this species.

Collections made in 1960 and 1974 show distinct ecological differences between *Oreohelix jugalis, O. vortex,* and *O. intersum*. Dissections of the first two confirm species separation of these and *O. junii*. *O. intersum* is considered to be distinct on the basis of its differing ecology and very different shell structure. The evidence for these statements follows.

Oreohelix jugalis (Hemphill, 1890)

(Figures 6a, 7b, *31* to *36*)

Patula strigosa var. *jugalis* Hemphill, 1890, Nautilus 3 (12): 134 – Banks of Salmon River, Idaho.

Oreohelix jugalis (Hemphill), Pilsbry, 1934, Proc. Acad. Nat. Sci., Philadelphia **85**: 398; Pilsbry, 1939, Land Mollusca N. America **1** (1): 496-497, fig. 322, a-c; Smith, 1943, Proc. Calif. Acad. Sci. (4) **23** (36): 538 – piles of water-worn boulders near the West bank of the Salmon River, one mile north of Riggins, Idaho Co., Idaho.

Oreohelix strigosa jugalis (Hemphill), Hanna and Smith, 1939, Proc. Calif. Acad. Sci. (4) **23** (25): 385-386, pl. 35, figs. 1-3.

Localities: Riverside pile of boulders, 1.6 km north of Riggins (FMNH 117882, April 21, 1960 and NMC August 17, 1974); east bank of Salmon River, 4.8 km north of Riggins and 640 m south of Lighting Creek (FMNH 117899, April 22, 1960); base of cliff, 45 m inland, about 2.4 km south of Chair Creek, north of Riggins (FMNH 170742, August 19, 1974).

Remarks: Local residents of Lucile found a few live stranded examples in river drift from the Salmon River at Lucile immediately following the record Spring floods of 1974, but none could be located in the same drift piles during August 1974. Pilsbry (1934: 398) suggested that the type locality be restricted to Lucile, but the finding by Smith (1939) makes the boulder area north of Riggins the logical site for a restricted type locality. All of the known localities are from large boulder piles or cliff base talus within the flood zone of the Salmon River.

Size and shape variation of adult specimens from the three recent sets is summarized in Table 4. The differences between the Lighting Creek and Riggins samples are significant for several parameters. With 94 degrees of freedom, "*t*" is 3.2028 for height, 3.2601 for diameter, 2.5854 for whorl count, and 3.0570 for umbilical width. In size, these amount to 4.4-6.5% differences compared to 3.8-8.9% differences in *Oreohelix **waltoni*** for similar charac-

Table 4

Variation in shells of *Oreohelix jugalis* (Hemphill)

Locality	1 mile north of Riggins	0.4 miles south of Lighting Creek	1.45 miles south of Chair Creek
Date collected	IV-21-1960	IV-22-1960	VIII-18-1974
Museum #	(FMNH 117882)	(FMNH 117899)	(FMNH 170742)
Number of adults	16	82	4
Height	12.64 ± 0.23 (11.0-14.4)	11.87 ± 0.10 (9.65-14.2)	11.78 ± 0.50 (10.6-13.0)
Diameter	22.18 ± 0.27 (20.4-25.0)	21.25 ± 0.11 (19.3-24.0)	22.4 ± 0.70 (20.9-24.0)
H/D ratio	0.570 ± 0.008 (0.521-0.613)	0.559 ± 0.003 (0.478-0.666)	0.525 ± 0.007 (0.507-0.542)
Whorls	5.98 ± 0.07 (5½-6⅜)	5.81 ± 0.03 (5⅜-6¼)	5.73 ± 0.06 (5⅝-5⅞)
Umbilical width	6.69 ± 0.15 (5.6-7.5)	6.39 ± 0.06 (5.0-7.8)	6.59 ± 0.38 (5.6-7.3)
D/U ratio	3.33 ± 0.06 (2.97-3.87)	3.34 ± 0.03 (2.81-4.02)	3.42 ± 0.14 (3.25-3.83)

ters. The greater differences seen between populations of *O. waltoni* (Table 3) and *O. strigosa* (Table 2) presumably reflect the less variable habitat in the deep talus rock piles near the river bank when contrasted with the less sheltered, drier sites occupied by the other two species.

The genitalia of *Oreohelix jugalis* (Figure 7 *b*) show a relatively short penis (P) with epiphallus (E) more than half its length. The ovotestis lobe (G) size and angling also differ from the structures seen in *O. vortex* (Figure 2 *b*). Internally, the penis of *O. jugalis* (Figure 6 *a*) shows a very short pustulose area and altered pilaster arrangement within the epiphallus (EPP). This contrasts greatly with the long pustulose area in *O. vortex* (Figure 6 *b*). In addition, the position and size of the penial verge (PV) is quite distinctive in the two taxa. The idea that *O. junii* might be closely related (see Pilsbry, 1939: 495) is partly supported by the anatomical data. That species has a much longer, reflexed penis (Pilsbry, 1939: 485; fig. 315, 14, 15, 15a) in which the ribbed section is more than half the penis length. The penis of *O. jugalis* is very short and the difference from that figured for *O. junii* probably is indicative of full species level difference. Both species seem to be grouped properly with the *O. subrudis* (Pfeiffer, 1854) series.

The radula of *Oreohelix jugalis* (Figures *31 - 36*) shows many differences from that of *O. vortex* (Figures *20 - 24*). In the former species, the central tooth (Figures *31, 33*) has only slight traces of ectocones, while in *O. vortex* (Figure *21*) they are well developed. *Oreohelix jugalis* has unicuspid laterals (Figures *31, 33*) with an occasional lateral bulge instead of the prominent ectocones of *O. vortex* (Figure *21*). The lateromarginal transition in *O. jugalis* (Figure *32*) involves first a slight indentation, then formation of a recognizable ectoconal cusp. Marginal teeth of *O. jugalis* (Figures *34, 36*) show a strong tendency towards multiple serrations on the ectocone, compared with simple ectocones on the outer marginals in *O. vortex*. The anterior margins of lateral teeth in *O. jugalis* (Figures *31, 32*) are longer and show a greater angulation than do the margins in equivalent teeth of *O. vortex* (Figures *21, 22, 23*). Worn central and lateral teeth of *O. jugalis* (Figure *35*) show that the wear occurs on both the cusps and anterior margins of the teeth.

Oreohelix vortex Berry, 1932

(Figures 1, 2b, d, 5b, 6b, *11, 20 - 24*)

Oreohelix vortex Berry, 1932, Pomona Jour. Ent. Zool. 24 (4): 57-58, figs. 1-2 – Salmon River, White Bird, Idaho Co., Idaho; Pilsbry, 1939, Land Mollusca North America 1 (1): 497-499.

Oreohelix flammulifer Berry, 1932, Pomona Jour. Ent. Zool. 24 (4): 58-60, figs. 3-4 – Salmon River, White Bird, Idaho Co., Idaho.

Berry (1932) presented measurements of these specimens, which were originally collected by Henry Hemphill. Both an avid collector and shell dealer, Hemphill's specimens are widely dispersed through many museum and private collections. A statistical summary of Berry's measurements is presented in Table 1. While the differences between the sets of *Oreohelix vortex* and *O. flammulifer* are highly significant in respect to height (with 17 degrees of freedom, "*t*" is 3.0560), diameter ("*t*" is 6.07576) and D/U ratio ("*t*" is 4.8687) and range from 7.8-13.3% of the smaller mean, the range of both sets is included within the sample (FMNH 117894) collected at White Bird in 1960. Berry's sets could be duplicated by pulling selected specimens from the latter set. Intergrades between *O. vortex* and *O. flammulifer* are numerous, hence I agree with Pilsbry (1939: p. 498) that they are synonyms.

Oreohelix vortex has a proportionately much longer penis and vaginal region (Figure 5 *b*) than *O. jugalis* (Figure 7 *b*). The latter has about 7 embryos in the uterus, compared with 4 in *O. vortex*. Internally, the penes (Figure 6, *a, b*) differ markedly, with the ridged and pustulose area equal in *O. jugalis* and the ridged area much shorter in *O. vortex*. The radular central and laterals are unicuspid in *O. jugalis* (Figures *31 - 33*) and tricuspid in *O. vortex* (Figures *21 - 23*). They are distinct species.

Explanation of Figures *31* to *36*

Oreohelix waltoni Solem, spec. nov.

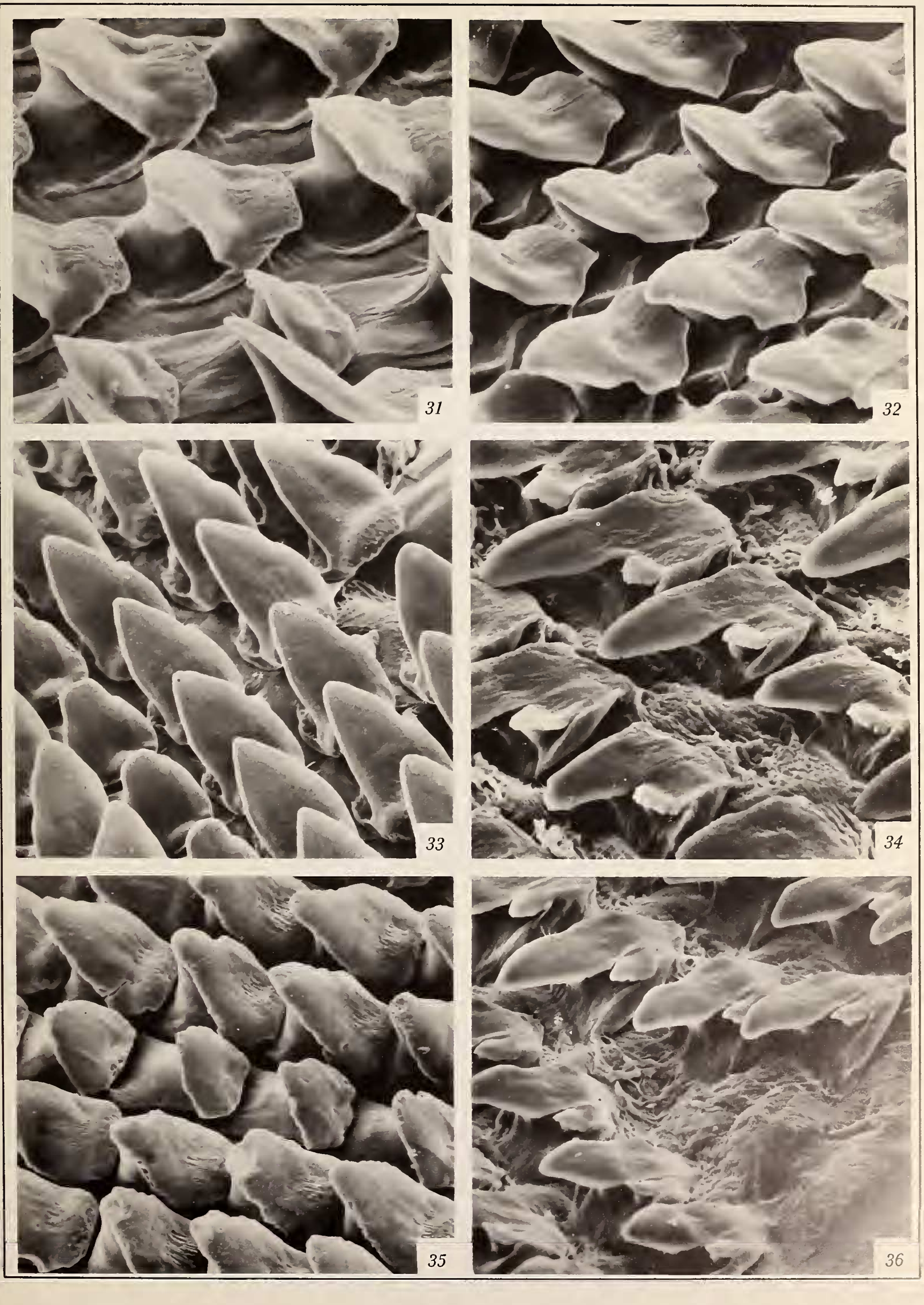
John Day Creek, north of Lucile, Idaho County, Idaho. Collected August 18, 1974 by A. Solem and A. Clarke. FMNH 170741

Figure *31*:	Central and early lateral teeth	× 877
Figure *32*:	Transition from lateral to marginal teeth	× 870
Figure *33*:	Central and early lateral teeth	× 475

Oreohelix jugalis (Hemphill, 1890)

East bank of Salmon River, 2.320 km south of Chair Creek, cliff base 45 m inland, Lucile, Idaho County, Idaho. Collected August 19, 1974 by Alan Solem. FMNH 170742

Figure *34*:	Outer marginal teeth	× 1480
Figure *35*:	Worn central and lateral teeth	× 510
Figure *36*:	Midmarginal teeth	× 850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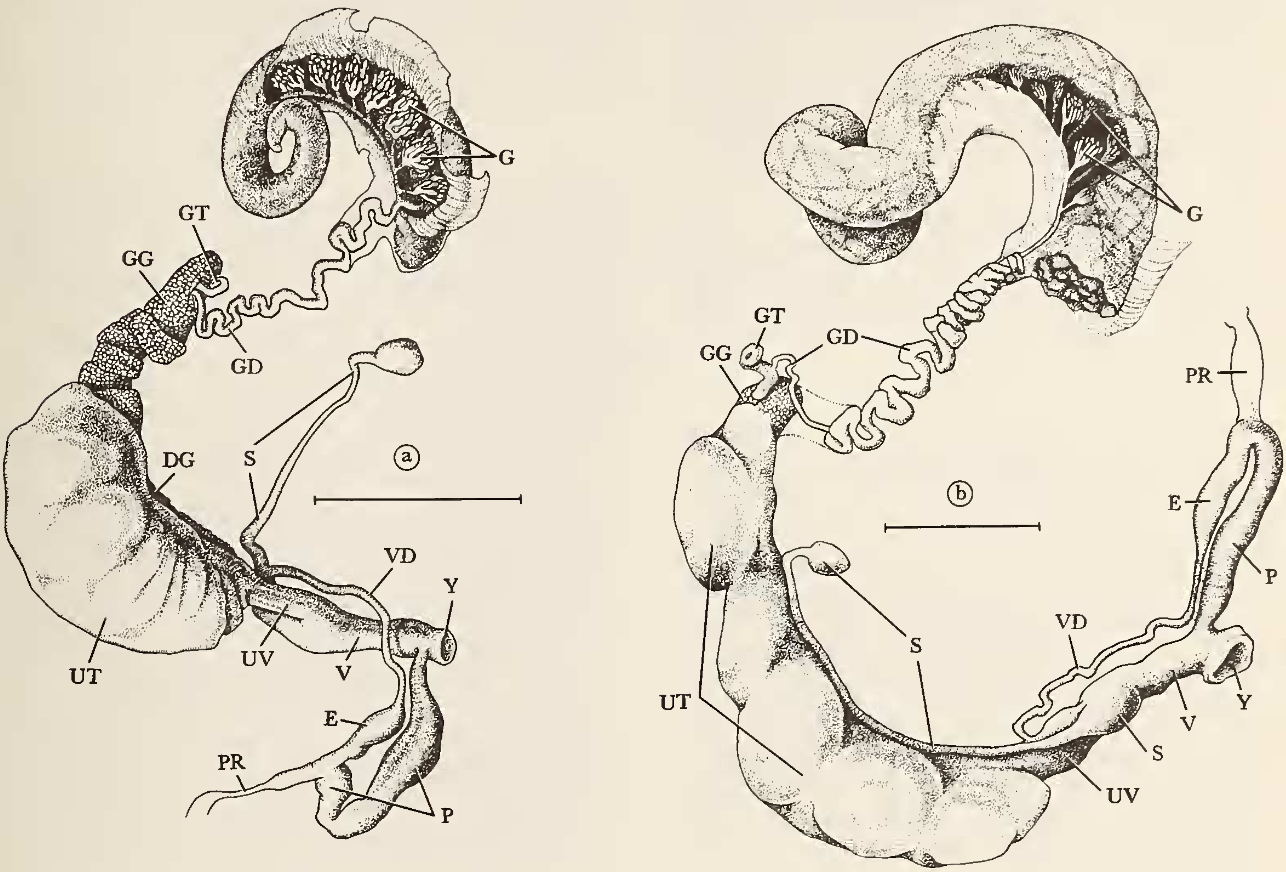

Figure 7

Genitalia: *a, Oreohelix idahoensis idahoensis* (Newcomb, 1866). FMNH 170712. Near Lucile, Idaho. Collected August 18, 1974; *b, Oreohelix jugalis* (Hemphill, 1890). FMNH 170742. Cliff base south of Chair Creek, near Lucile, Idaho. Collected August 19, 1974. Scale lines equal 5 mm

The total known habitat of *Oreohelix vortex* extends for less than 150 m along a bluff. Within this area, both it and *O. strigosa* are common, but the total population is relatively small in size. Because of this, the exact location of the colony is not published.

Oreohelix intersum (Hemphill, 1890)

Patula strigosa var. *intersum* Hemphill, 1890, Nautilus 3 (12): 135 – bluffs along the banks of little [sic] Salmon River, Idaho.

Oreohelix intersum (Hemphill), Berry, 1932, Journ. Ent. and Zool. Pomona College 24 (4): 62; figs. 9-10; Hanna & Smith, 1939, Proc. Calif. Acad. Sci. (4) 23 (25): 388-389; plt. 36, figs. 1-3.

Oreohelix jugalis intersum (Hemphill), Pilsbry, 1934, Proc. Acad. Nat. Sci., Philadelphia 85: 398, 406; Pilsbry, 1939, Land Mollusca N. America 1 (1): 499; figs. 322, d, e.

Remarks: The habitat of this species was well defined by Hemphill (1890, p. 135) as "... inhabits stone piles at the foot of a steep bluff some distance from the river." Just up-stream from where the Little Salmon River joins the main stream, the west bank has a moderate flood plain extending to heavy talus on a steep bluff. For several miles south of Riggins, these talus slopes contain colonies of *Oreohelix intersum*. The slides are very deep and the snails apparently migrate seasonally, since in April specimens were common near the talus surface, but in August only dead examples were found in the same slides.

The higher spire, narrow umbilicus, development of relatively prominent radial ribbing, weak keel, and deep slide habitat are sufficient reasons to grant this taxon specific level status. No live collections containing embryos were available, so I did not dissect and illustrate the April 1960 material.

SUMMARY

Dissection and analysis of differences for two sympatric species, *Oreohelix strigosa strigosa* (Gould, 1846) and *O. vortex* Berry, 1932 provide data concerning the significance of variations observed in penial structure throughout the genus. *Oreohelix* ***waltoni*** Solem, spec. nov. from John Day Creek, Lucile, Idaho is described. The anatomy and radular structure are illustrated and compared with that of *O. idahoensis* (Newcomb, 1866). Taxa formerly listed as subspecies of *Oreohelix jugalis* (Hemphill, 1890) are discussed, with dissections, radular examination with the SEM, and ecological differences showing that *O. jugalis* (Hemphill, 1890), *O. intersun* (Hemphill, 1890), and *O. vortex* Berry, 1932 are distinct species.

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